Dynamic biological adhesion: mechanisms for controlling attachment during locomotion

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The rapid control of surface attachment is a key feature of natural adhesive systems used for locomotion, and a property highly desirable for man-made adhesives. Here, we describe the challenges of adhesion control and the timescales involved across diverse biological attachment systems and different adhesive mechanisms. The most widespread control principle for dynamic surface attachment in climbing animals is that adhesion is 'shear-sensitive' (directional): pulling adhesive pads towards the body results in strong attachment, whereas pushing them away from it leads to easy detachment, providing a rapid mechanical 'switch'. Shear-sensitivity is based on changes of contact area and adhesive strength, which in turn arise from non-adhesive default positions, the mechanics of peeling, pad sliding, and the targeted storage and controlled release of elastic strain energy. The control of adhesion via shear forces is deeply integrated with the climbing animals' anatomy and locomotion, and involves both active neuromuscular control, and rapid passive responses of sophisticated mechanical systems. The resulting dynamic adhesive systems are robust, reliable, versatile and nevertheless remarkably simple.

In contrast to conventional man-made glues, the adhesive systems of many animals can be switched rapidly between strong attachment and easy detachment, enabling locomotion in environments that require firm surface attachment, such as the canopy of forests, or the intertidal zone. Throughout the lifetime of a climbing animal, such cycles between strong attachment and rapid detachment have to occur millions of times with no loss of adhesive force [1]. The ability to control adhesion is therefore a fundamental property of natural adhesive systems. Indeed, four out of the seven benchmark properties for the performance of gecko adhesives defined by Autumn [2], relate to the controllability of adhesion (namely, anisotropic attachment, low detachment force, non-sticky default state, high pull-off to preload ratio; the remaining three are self-cleaning, anti-self-matting, and material independence). As controllability is also a highly desirable feature for synthetic adhesives, animal adhesive structures have become models for worldwide efforts to fabricate controllable 'biomimetic' adhesives, which may have a wide range of applications, including but not limited to industrial pick up-and-release manipulation at the macro- and microscale, and climbing robots [for recent reviews, see 3–5].

An adhesive system is 'controllable' if large variations in adhesive force can be achieved via the variation of system parameters, and 'dynamic' if such changes can be realised within short periods of time. In biological adhesive systems, these changes are not merely binary, but many animals can adjust their attachment systems in a gradual manner to respond to external forces resulting from climbing on substrates with various slopes, and from waves, wind, or additional loads [6–12]. In this article, we provide a brief overview of the mechanisms which allow adhesion control in biological adhesive pads.

Control of adhesion: from permanent glues to dynamic adhesives

Attachment and detachment of adhesive contacts is a fundamental requirement for locomotion. Protraction of one body part, such as a leg or part of a foot, requires other body parts to remain in contact, in order to resist gravity or other external forces, and to produce the forward thrust which powers locomotion. The feet of moving animals go through a coordinated cycle of 'stance' and 'swing', and at the start and end of each stance phase, the adhesive contacts will have to be formed and broken.[1]

Although the time required to form and release adhesive contacts may often represent only a fraction of the stance and swing phase, it is likely that at least in some animals, the speed of attachment and detachment imposes a limit to the stepping frequency and hence the speed of movement. Animal adhesive systems range from permanent to highly dynamic, reflecting the animals' lifestyle and speed of locomotion. Table S1 in the supplementary information (SI) summarises the limited data available on the timing of stance-swing cycles in animals that use adhesion during locomotion. Temporary adhesion is used by animals differing in "stride frequency" (defined here as the inverse of the time of one complete pad attachment-detachment cycle) by more than two orders of magnitude (see also Fig. 1). This large variation in stride frequencies may be based on several factors, including the medium in which the adhesive organs operate (air or water), the adhesive mechanism, and the dimension of individual adhesive contacts.

Permanent attachment is predominantly achieved by glues, which allow animals to remain firmly attached in the same place for extended periods of time [e. g. sessile marine an-

[1]During the locomotion of some gastropods, muscular waves moving along the underside of the foot switch different parts of the foot between stationary adhesive contact ('stance') and forward sliding over mucus ('swing'), so that the protracted part is not completely detached but remains in surface contact [13].

Figure 1: Animal adhesive systems range from permanent to temporary and highly dynamic. While permanent adhesive systems are glue-based, slow temporary adhesive systems use releasable glues or suction, and the most dynamic adhesive systems employ interfacial forces. Image sources are provided in the SI.

imals including sponges, cnidarians, cirripede crustaceans, bivalves, polychaetes, bryozoans and tunicates, but also terrestrial phoretic mites and insect pupae that attach themselves to substrates, see ref. 14–16]. Glues may be defined as secretions, often consisting of multiple components, which are applied in liquid form, but then solidify in contact with the substrate. Well-studied systems include the byssus thread of mussels, and barnacle cement [17]. However, glues do not have to be permanent, and indeed are also used for locomotion in temporary underwater adhesive systems. For example, flatworms and echinoderms achieve repeated attachment and detachment by the subsequent release of adhesive and de-adhesive secretions, each produced by distinct glands or cells [14, 18–20]. Glue-based adhesion and de-adhesion require (i) the secretion of the adhesive, (ii) contact formation, (iii) solidification, (iv) secretion of the release agent, (v) its diffusion into the adhesive, and (vi) reaction with it. Contact formation in particular is a key challenge for adhesive systems employed in water, as it requires water to be removed beneath the adhesive organ. Water is initially squeezed out via hydrodynamic forces, but complete removal by dewetting requires the thin remaining water films to be thermodynamically unstable, which is unlikely for many polar natural substrates [21]. Some mussels and cyprid larvae can displace water via the secretion of lipids into the contact zone instead [22, 23]. As an alternative, viscous secretions such as the glycoprotein footprints of temporarily adhering cyprid larvae may strengthen underwater adhesion by effectively replacing the water film [24].

The numerous steps involved in attachment-release cycles of glue-based adhesives are time-consuming, and probably only feasible if diffusion distances are short; even for microscopic contacts they may therefore impose a speed constraint on attachment-detachment cycles. Water displacement, secretion of lipids or glycoproteins, and viscous adhesion will result in further speed constraints, together explaining why glue-based adhesive systems of aquatic animals are generally less dynamic than those of terrestrial animals that do not rely on glues (TableS1). One strategy to reduce the time needed for underwater attachment and detachment may be the miniaturisation of individual adhesive contacts (as seen in flatworms and cyprid larvae; TableS1), which helps to accelerate both fluid drainage and diffusion-based processes [24, 25].

A potentially faster type of controllable attachment is suction, which lacks the speed and size constraints of diffusion. A clear definition of suction for biological attachment systems is still missing (and beyond the scope of this review); here we use the term to refer to attachment produced by reducing the pressure beneath the attachment organ, excluding pure capillary or viscous adhesion. Suction in this sense is used by diverse primarily aquatic animals including limpets, leeches, clingfish, remora fish, water-fall climbing gobies, octopus, squid, net-winged midge larvae, and diving beetles [26–34]. These animals produce suction either by muscular action (active suction), or by the recoil of elastic elements (passive suction). Both strategies have in common that they tend to expand the volume underneath the suction organ. Suction organs share with other underwater adhesive systems the need to drain water from the outer rim of the contact zone, in order to achieve a tight seal. However, they are likely more tolerant to small amounts of residual water, as even leaky suction organs can allow for sufficient attachment over the timescales required for locomotion, and leakage rates can be reduced by the secretion of mucus [34]. In fact, the almost exclusive occurrence of suction among aquatic animals probably arises because the presence of an incompressible fluid such as water or mucus beneath the suction cup has the advantage that large variations in pressure can be produced by miniscule displacements. Whereas suction in air is limited by the atmospheric pressure, water can also resist tensile forces, so that even negative pressures can be achieved [27].

Little is known about the mechanisms of detachment in natural suction organs. Generally, voluntary detachment takes place once the reduced pressure inside the sucker cavity is neutralised; the fastest way for this to occur may be by relaxation of the muscle(s) that produce(s) the suction for 'active' suction systems, but movements by other muscles might be needed to release passive suction. In net-winged midge larvae (*Blephariceridae*), attachment is achieved by raising a 'piston' in the centre of the suction disc. Detachment, in turn, can occur by rapidly 'flooding' the sucker through the opening of a V-shaped notch located at the anterior rim of the disc, with the piston still in its upper position [41].

By far the most dynamic control of adhesion occurs in adhesive systems which rely on interfacial forces, including both 'dry' van der Waals interactions and 'wet' capillary forces. Most terrestrial climbing animals belong to this category [a contribution of van der Waals forces has also been discussed for the temporary underwater adhesion of barnacle cyprid larvae, see ref. 24]. There has been substantial convergence both in the morphology of the adhesive systems of terrestrial climbing animals, and in the control mechanisms they employ [12, 42–53]. Detachment in these adhesive systems does neither require chemical release agents (as for glues), nor muscular action to neutralize pressure gradients (as for suction). Instead, rapid control of adhesion is achieved through mechanical systems. The universal strategy for rapidly reversible attachment is the control of adhesion via shear forces, which we review in detail in the following sections.[2]

Control of adhesive forces in dynamic biological adhesive systems

The maximum force an adhesive can carry is the product of its adhesive strength, and the area of contact. Animals could thus potentially control how well they adhere in two ways: first, they could alter the fraction of the available

[2]Many insects possess several attachment pads per leg. Unless otherwise stated, we are referring to distal adhesive pads in this review, and only briefly discuss the role of proximal friction pads.

Figure 2: In all non-aquatic animals climbing with adhesive pads tested to date, adhesion, F_A, is approximately half of the shear force, F_S, acting during detachment (see panel (d)); the dashed line visualises this approximate 'rule of thumb', which appears to hold for (a) geckos [*Gekko gecko*, seta, array and toe-level data; 35, 36], (b) tree frogs [*Litoria caerulea*, whole body data; 37], (c) dock beetles (*Gastrophysa viridulae*, single pad data, D Labonte & JMR Bullock, unpublished data), (e) stick insects [*Carausius morosus*, single pad data; 38], (f) cockroaches [*Nauphoeta cinerea*, single pad data; 39], and (g) ants [*Oecophylla smaragdina*, single pad data; 40]. Shear force therefore appears to be a universal control mechanism independent of pad morphology (smooth or hairy), adhesive mechanism (wet or dry), or contact size. Detailed regression results for (a-c) & (e-g) can be found in the SI.

adhesive area which they bring in contact with a surface; second, they could vary the strength of the contact, i. e. alter the force required to detach a unit area of their sticky pads.

In dynamic biological adhesive systems, the universal control parameter for both variables is shear force, i. e. a force acting in parallel to the adhesive interface. The typical effects of shear force on contact area, adhesive strength and hence net adhesive force can be summarised as follows: 'Pushing' pads away from the body results in an unstable contact, reflected in a dramatic decrease in contact area and thus effortless detachment, whereas 'pulling' pads towards the body results in a stable or increasing contact area, and strong attachment [54–60]. This 'shear-sensitivity' of adhesion is widespread across terrestrial climbing animals, including flies [54, 61, 62], spiders [12, 63], bees [55], bush-crickets [64], geckos [2, 35, 36, 65], stick insects [38, 57, 60], bats [66], cockroaches [52, 58], ants [11, 55, 67], leafhoppers [68], tree frogs [37, 38, 69], and beetles [49, 57]. Climbing animals can therefore control attachment simply by shearing their adhesive pads along the surface; pulling results in strong attachment, whereas pushing enables easy detachment (an important exception to this rule are 'friction pads'; see below).

Control of adhesive strength

In all adhesive pads of climbing animals tested to date, the adhesive force, i.e. the perpendicular force required to detach the pads, increases when pads are pulled towards the body [35–38, 52, 60]. As a rule of thumb, the adhesive force is approximately half the shear force applied during detachment [Fig. 2. See 36, 38]. This empirical rule holds for large or small, 'wet', 'dry', 'smooth' or 'hairy' adhesive systems tested with various methods, suggesting the presence of a universal control mechanism that is independent of contact size, adhesive mechanism, pad morphology, and experimental method (see Fig. 2). Importantly, the increase of adhesion with shear force arises from an increase in adhesive strength, and not solely from changes in contact area [37, 52, 60, 70]. While this characteristic shear-sensitivity of biological adhesive pads is empirically well-established, the exact mechanism(s) through which shear forces increase contact strength are still unclear. Why is this relationship approximately linear, and why is the slope of this linear relationship 0.5? To the best of our knowledge, there is currently no theoretical model which predicts these peculiar features from first principles [36, 38].

The most successful theoretical attempts at explaining the shear-sensitivity of biological adhesive pads have been based on tape peeling theory, which likens the pads to thin strips of adhesive tape [37, 38, 71–73, See Fig. 3 A-C]. Based on peeling theory, the effect of shear forces may be understood qualitatively as follows [for a quantitative discussion, see 38]: breaking adhesive contacts increases the system's total energy, as it creates new surfaces. This energy per unit area, G, is 'paid for' by the work done when the point of force application moves by a distance δ whilst detaching a unit length L_0 of tape (see Fig. 3 D). In this framework, climbing animals can hence increase the adhesive force F_A by (i) increasing G; or (ii) reducing δ. Actively applying a shear force makes good use of both options in at least three different ways:

First, as the shear component of the applied force is increased, the pads peel at lower angles ϕ. For a perpendicular pull-off, $\delta = L_0$, but for pull-offs at lower angles, the point of force application only moves by a fraction of the peeled tape length, $L_0(1 - cos(\phi))$, so that $\delta \leq L_0$ [74, see Fig. 3 D]. Thus, a larger force F must be supplied to provide the same amount of work. To resist detachment, animals can hence reduce $\delta/L_0 = 1 - cos(\phi)$ by decreasing ϕ, i. e. by actively pulling their pads inwards. This effect is based purely on geometry.

Unfortunately, there is a limit to this strategy: detached parts of the pads stretch, and this stretch increases δ [75, see Fig. 3 E]. As the amount of work done for stretching the pad is larger than the associated increase in elastic strain energy [75], stretching reduces the force required to peel off the pads. For soft and thin biological adhesive pads, this effect would severely limit the positive effect of applying a shear force.

It is here where the second effect comes in: large shear forces eventually result in pad sliding, which also strains *attached* parts of the pads prior to detachment [38, Fig. 3 F]. Upon detachment, these 'pre-stretched' pads then stretch less than unstretched pads, reducing the negative impact of stretching outlined above. This second effect is thus based on 'energy dissipation' [38, 65, 76]: The work done for pad stretching does not help to create new surfaces, but is instead balanced by the frictional work done when pads are stretched while still in contact with the surface [38, 76]. Here, shear-sensitive biological adhesives differ fundamentally from many commercial high-strength adhesives, as they dissipate energy at the interface (via friction) instead of the bulk (via cavitation, viscoelastic fingering etc) [38, 65, 77].

The effect of (i) a decrease in peel angle, and (ii) stretching attached parts of the tape have both been included in quantitative models [38, 73–76, 78], which show good agreement with experimental data on biological adhesive systems [37, 38]. However, data for stick insects showed that this agreement was limited to peel angles larger than approximately 30°. For smaller peel angles, adhesive forces systematically exceeded theoretical predictions [38]. There hence must be a third effect. In contrast to the first two effects, which reduce δ, this effect must reflect an increase

Figure 3: (A) Due to the sprawled-leg posture of most climbing animals, externally applied attachment forces result in the application of both a normal and a shear force at the level of individual pads (illustrated in (B); climbing animals can also apply shear forces actively). These shear forces make it harder to detach the pads, and this 'shear-sensitivity' can be partially understood through peeling models (C), which liken adhesive pads to thin strips of adhesive tape, with width w, peeled at an angle ϕ. (D) As a unit length L_0 of the tape is peeled, the point of force application moves by a fraction of this distance. Because this fraction decreases with decreasing peeling angle (or increasing shear force component), more force needs to be supplied to do the required work, leading to an apparent 'strengthening' of the contact. (E) Biological adhesive pads are thin and soft, and therefore likely stretch upon detachment (strain ε). This stretching increases the work done upon detachment, so reducing the effect outlined in (D). (F) The negative effect of pad stretching can be circumvented if the tape is stretched *prior* to detachment ('pre-strain' ε_0). Storing strain energy in attached parts of the tape can not only make involuntary detachment harder, but also aid rapid voluntary detachment. A more detailed discussion is provided in the text.

in G, which may be understood as follows: The positive effects of pad sliding are bound by the geometrical limit $\delta \leq L_0 - L_0 \cos\phi$, i. e. the distance moved for a unit length of tape which does *not stretch at all* upon detachment (a more formal proof is presented in the SI). While pad sliding can thus make even thin and soft pads behave as if they were effectively inextensible [38], the peeling model for such tapes only predicts a square-root dependency of adhesion on shear force [in the limit of large shear forces, see 38, 52]. As the observed relationship is linear, the only way to reconcile peeling theory with the experimental data is therefore a shear-induced increase in G.

In stick insects, the departure from peeling theory coincided with the onset of whole-pad sliding [70], so that it appears plausible that sliding results in an increase of G. Two hypothetical mechanisms could explain such an increase: first, sliding may result in triboelectric charging. However, the relationship between adhesion and friction remained unaltered on conducting surfaces [70], suggesting that triboelectric effects do not play an important role; second, sliding can rapidly deplete liquid films in the contact zone [79], and such changes in film thickness may cause an increase in G [38, 77]. Indeed, recent experiments suggested that the contact-mediating secretion found in all insects studied to date acts as a 'release layer', consistent with this hypothesis [77, 80]. However, fluid depletion should only occur in animals with wet adhesive systems, so that we would still be lacking an explanation for identical data on dry adhesive systems [36].

Clearly, more theoretical and experimental work is required to quantitatively explain the approximately linear relationship between adhesion and friction in biological adhesive systems. The sharp drop of adhesion for peel angles $> 30°$ is biologically important, as it allows animals to use relatively small movements to switch from weak to strong adhesion. Clarifying the basis for this most fundamental adhesion control mechanism across climbing animals should therefore be a core area for future research.

Control of contact area

Changes in contact area occur by definition during attachment and detachment, but as any soft object increases its contact area when pressed against a substrate, and decreases it during pull-off, not all such changes correspond to an active control mechanism. In the following discussion, we will therefore focus on non-trivial contact area changes in two scenarios: in the context of *attachment*, we will describe active and passive adjustments of the contact area which occur rapidly as a direct result of increased loading requirements. In the context of *voluntary detachment*, we will discuss strategies through which the contact can be broken by other means than the supply of a force normal to the surface.

Active and passive control of attachment

In technical adhesives, contact formation is typically achieved via the application of a force perpendicular to the interface. In sharp contrast, the contact area of dynamic biological adhesive systems can be controlled via shear forces. An increase of contact area in response to shear forces towards the body has been found across most dynamic adhesive systems of climbing animals studied to date, despite the striking diversity of adhesive pad morphologies. For example, the smooth footpads of ants and bees can unfold passively (without any muscular action) when the retracted pad in surface contact is dragged towards the body [55, 67]. The adhesive footpad of stick insects is not foldable, but possesses an internal fibrillar ultrastructure, which hydraulically translates longitudinal pulls into a lateral expansion of the adhesive contact zone [81]. The hairy adhesive pads of lizards, many arachnids and diverse insects, in turn, possess spatula-shaped tips with a non-adhesive 'default' (non-contact) position, i. e. they are not parallel to the substrate. Only when setae are sheared towards the body, do the tips bend and come into full contact [36, 49, 82, 83]. Importantly, these increases in contact area with shear forces are not an all-or-nothing reaction. Stronger shear forces generally lead to larger contact areas, until the contact zone has reached its maximum size [55, 68], allowing a gradual adjustment to external loads. Such gradual contact area adjustments can be made actively, i. e. via the contraction of muscles pulling feet inwards (or pushing them outwards), but they can also arise passively. Because of the sprawled posture of climbing arthropods and vertebrates, legs are pulled inward automatically by the animal's body weight during inverted climbing (or pushed outward during horizontal locomotion); during vertical climbing, legs above the body centre of gravity (CoG) will be pulled automatically, whereas those below will be pushed. External forces resulting from wind, rain, or from carrying load, further add to the shear force arising from the animal's own body weight.

Because shear forces arise passively in situations where strong attachment is required, shear-sensitivity ensures an 'automatic' engagement and activation of the adhesive organs. Indeed, it is no coincidence that adhesion control is both active and passive. Neuromuscular control of attachment and detachment is essential for climbing, and for

adjusting to different environmental conditions, substrate geometries and textures [84, 85]. However, passive mechanisms simplify the complexity of the active feedback control that needs to be mastered for successful climbing [86], and a purely mechanical response triggered by shear forces can result in extremely rapid increases in adhesive contact area. For example, the pad contact area of the smooth adhesive pads of weaver ants and stick insects can double within less than a millisecond of a perturbation [37]. Even for small animals such as insects, any control via active neuromuscular 'reflexes' would take at least an order of magnitude longer. The virtually instantaneous 'preflex' is hence essential for preventing detachment during rapid and unpredictable perturbations (such as raindrops or wind gusts), and avoids the need to use large contact areas and therefore high detachment forces during locomotion. In practice, contact area is thus likely controlled by a combination of passive and active loads. Indeed, in cockroaches walking upside-down, loading triggers the activation of the tibial flexor muscle which mediates an inward pull of the legs [87], suggesting a coupling between active and passive control mechanisms.

While likely the dominant mechanism, shear forces are not the only way in which the adhesive contact area can be controlled. Some climbing animals are also capable of directly influencing the adhesive contact zone by muscular control. For example, contraction of the claw flexor muscle in insects and spiders can not only bring adhesive pads into surface contact, but also induce local deformations of the cuticle which increase the size of the contact zone; its relaxation in turn can drive the pad's detachment [6, 55, 62, 67, 86, 88, 89, and see next section]. Recent findings show that adhesive pads of tree frogs contain bundles of smooth muscle fibres which may be involved in the direct control of adhesion [90].

Rapid detachment via release of elastic energy

Voluntary detachment during climbing locomotion has to occur rapidly, and should consume minimal amounts of energy. Both needs are at least partly met through an inbuilt release mechanism which arises as a direct consequence of pad *engagement*: Due to the shear-sensitivity of their pads, climbing animals need to pull their legs inwards in order to resist detachment. As outlined above, the resulting shear forces cause deformations of the attachment structures which typically increase the adhesive contact area. For example, shear forces straighten curved adhesive setae or the tarsus as a whole [49, 65, 67, 86], bend adhesive hair tips or internal rod-like structures [49, 64, 81], unfold smooth pads or expand their cuticle along the transverse axis [55, 81], and likely stretch pads and adhesive hair tips along the longitudinal axis [38, 81, 91–93]. All these deformations bring with them the storage of elastic energy, which, upon removal of the shear force, can help breaking the contact, and even result in spontaneous detachment of the pads in the absence of external forces [65, 73, 93].

An intuitive way to understand how storing elastic energy can result in spontaneous detachment is to think of a pad as a thin strip of adhesive tape, which is stretched to a 'pre-strain' ε_0 prior to or during surface attachment. If the elastic energy stored in the stretched tape exceeds the decrease in surface energy associated with contact formation, the contact is unstable, because a detached but relaxed tape corresponds to a more favourable energetic state. In the SI, we show that spontaneous detachment of a tape requires a minimum pre-strain $\varepsilon_{\min} = \frac{1}{\zeta}\left(1+\sqrt{1+2\zeta}\right)$ (here, $\zeta = Eh/G$ is a characteristic dimensionless number representing the ratio between elastic and adhesive work done during detachment; h is the thickness of the tape, and E its Young's modulus). If this strain is exceeded, the tape can only adhere if *an external force is applied* [see also 73]. The somewhat complex relationship between contact stability and pre-strain can be visualised in 'stability envelopes', encompassing combinations of pre-strain and applied force for which stable attachment is possible (see Fig. 4). For $\varepsilon_0 < \varepsilon_{\min}$, these plots only have an upper bound, corresponding to the critical peel force. In this regime, detaching the tape always requires the application of a force. If $\varepsilon_0 > \varepsilon_{\min}$, however, the envelopes also have a lower bound, corresponding to the force required to stabilise the tape against spontaneous detachment [see SI and ref. 73]. In this regime, voluntary detachment can simply be triggered by *reducing* the applied force below this lower bound, causing the tape to peel spontaneously. Remarkably, pre-stretching hence not only enhances the resistance against forced detachment, but also provides a mechanism for fast and effortless voluntary detachment [73]. Storage of elastic energy during attachment to recover it for detachment helps to balance the contradictory demands of a strong yet easy-to-detach adhesive system, and may therefore be a key principle enabling controllable adhesion.

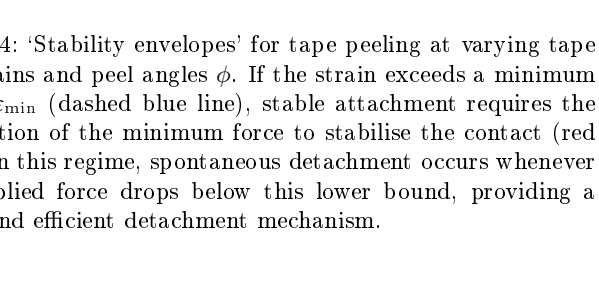

Figure 4: 'Stability envelopes' for tape peeling at varying tape pre-strains and peel angles ϕ. If the strain exceeds a minimum strain $\varepsilon_{\min}$ (dashed blue line), stable attachment requires the application of the minimum force to stabilise the contact (red line). In this regime, spontaneous detachment occurs whenever the applied force drops below this lower bound, providing a rapid and efficient detachment mechanism.

As compelling as these arguments may be, the extent to which climbing animals use 'pre-strain' to ease detachment remains largely unclear. Benefiting from the release mechanism described above requires $\varepsilon_0 > \varepsilon_{\min}$. For biological adhesive pads, the required strain levels are probably unrealistically large (for an estimated range of $1 < \zeta < 100$, $15\% < \varepsilon_{\min} < 273\%$. We provide a more detailed discussion of the limits of this model in the SI). Thus, longitudinally stretched pads are unlikely to be the sole provider of the elastic energy which drives detachment, but other deformations in pads and legs may be involved (see above). The compliance of the pads or such external structures needs to be fine-tuned to the system's demands, so as to enable sufficient elastic energy storage without requiring excessive stresses or strains [80]. More generally, adhesive pads may be designed so that unloading does not cause complete detachment but only facilitates it, as maintaining some active control over detachment may be adaptive to protect against unwanted detachment by perturbations. An example of an actively controlled detachment that does not appear to rely on the release of elastic energy is the detachment of gecko toes by digital hyperextension [94].

Contact mechanics affect organismal-level locomotion, and vice versa

Locomotion constrains how adhesive pads can be attached and detached, but surface attachment also influences locomotion. Comparisons of animals climbing on vertical, horizontal and inverted surfaces, as well as on non-slippery versus slippery substrates have revealed clear differences. Flies walking upside down showed a higher duty factor (average proportion of legs in surface contact) than when walking horizontally. While flies mainly used a tripod gait for horizontal walking, they switched to gaits with four or more legs in surface contact when climbing [95, 96]. Similar kinematic adjustments are seen in insects climbing on slippery substrates [e. g. waxy plant stems; see ref. 97], or following pad contamination [98]. In both cases, insects showed an increase in the duty factor, accompanied by a decrease in step frequency and walking speed. The detailed causes triggering these kinematic changes are still unclear; they may include both direct physical effects of gravity or slipping on locomotion, and sensory detection of substrate orientation, substrate texture or leg slip, followed by active adjustment of locomotion. Indeed, numerous sensors have been identified on the legs and tarsi of insects, which can detect substrate engagement and leg slip, and trigger the activation of the grip-enhancing claw flexor and tibial flexor muscles [85, 99, 100]. Sensory feedback is doubtlessly essential for adapting locomotion to changes in load and environmental conditions [87, 101].

The higher number of legs in surface contact during inverted climbing may simply provide insects with a proportional increase in adhesive capacity, but it may also be critical for attaching and detaching their shear-sensitive adhesive pads. A simple geometric rule that may always hold during slow inverted walking is that the projection of the body CoG onto the surface must be located within the polygon formed by the feet in contact. If this condition is met, all the legs in stance can be under tension and sheared inward simultaneously. This 'inverted stability' rule is equivalent to the rule for static stability during upright walking, which demands that the CoG has to fall within the polygon of support in order to avoid toppling [102]. In contrast to the rule of static stability, the minimum number of legs in surface contact for achieving stable inward shear is two [103]. However, under quasi-static conditions (and assuming that small insect pads can only produce negligible torques around their contact zones), at least four legs must be in surface contact to allow detachment of one leg by unloading or pushing. Hence, the higher number of legs in contact during inverted walking may not only increase adhesion, but also enable controlled detachment, and as such may arise as a direct consequence of the control mechanisms on the level of single adhesive contacts.

Pad detachment can be driven by the controlled release of elastic energy, but it can also be achieved by an increase of the peel angle, which strongly reduces adhesion as predicted by tape peeling models. As joint torques in running animals are typically minimized by keeping force vectors approximately aligned along the legs [104, 105], changing from a low to a high peel angle for detachment would require a corresponding movement of the leg. Such a 'rolling' motion (lifting the tarsus from the proximal side) is a 'normal' part of walking and running for the forward-oriented front legs of lizards and insects, but would be less natural for middle and hind legs, as it would require the animals to walk sideways or backward, respectively. Indeed, observations on ants and flies suggest that rolling is commonly used only by the front legs, whereas middle and hind legs mostly detach without such an angle change [40, 106].

While the shear sensitivity of adhesion allows animals to efficiently switch adhesion on and off during locomotion, it also leads to constraints. As adhesive pads detach easily when pushed, they are not suitable for transmitting forces in this direction. Both during horizontal running and vertical climbing, however, at least some of the legs have to produce pushing forces. Vertically climbing tree frogs and geckos can solve this problem by adjusting the orientation of their limbs and digits for head-up, head-down or lateral climbing, so that for each leg some toes are pointing upward, in the correct orientation to support the body weight by pulling [107–109]. Climbing arthropods, however, possess only one tarsus per leg. Similar to geckos and frogs, vertically climbing insects can re-orient their legs to some extent so that a larger proportion of their body weight is supported by legs above the body centre of gravity, where the adhesive pads are in the correct pulling orientation [110, 111]. However, using only the legs above the body CoG for climbing would impose a severe constraint on locomotion.

Many arthropods have therefore evolved distinct types of attachment devices on their tarsus, which allow them to push (see Fig. 5). For example, vertically climbing cockroaches engage the tarsal pads (euplantulae) in legs below the body CoG, but use the distal adhesive pad in legs above the CoG [58]. Similar observations have been made in beetles, stick insects, and crickets [60, 112, 113]. The ability to produce large pushing forces is particularly essential for insects performing explosive jumps by rapidly extending their hind limbs [68]. As pushing is typically coupled with positive normal forces, the proximal tarsal pads do not need to produce adhesion, but only high traction forces; they have therefore been termed *friction pads* (see Fig. 5). Single-pad force measurements in stick insects demonstrate that the biomechanical properties of friction pads can differ fundamentally from those of adhesive pads [60, 114]: while adhesive pads produce high adhesion when activated by shear forces, friction pads produce little adhesion, but high friction when activated by normal forces [60]. Because of the sprawled posture of arthropods, adhesive pads therefore automatically increase adhesion when exposed to pull-off forces, whereas friction pads automatically increase friction when exposed to shear during natural locomotion. Therefore, both types of pad may be thought of as 'self-stabilising'. Their mechanisms of attachment and detachment are also analogous: both store elastic energy during contact formation, the release of which then drives detachment.

The different functional adaptations of proximal friction pads and distal adhesive pads are also reflected in their anatomical position, which can be explained by the chain-like flexibility of the arthropod tarsus. As the tarsus buckles easily, the tibia can transmit large pushing forces only to the friction pads on the proximal tarsus, but not to the distal adhesive pads. However, the tarsus

Figure 5: Comparison of adhesive pads and friction pads in insects. Both pad types are specialised for resisting forces in different directions, and thereby serve fundamentally different functions. Adhesive pads are located distally on the foot, and produce high adhesion when activated by shear (pulling) forces, whereas friction pads are located proximally on the foot, and produce high friction when pressed against the substrate.

is a tensile structure, and can easily transmit a strong pull to the distal adhesive pads. As a result, pulling legs towards the body increases contact area for (distal) adhesive pads, but decreases the contact area of (proximal) friction pads; the opposite holds when legs are pushed [57, 58]. Because this anisotropy is at least partly based on the structure of the insect leg, it can be reduced by immobilising the tarsus and pre-tarsus. Such experimental manipulation strongly reduces or even reverses anisotropy in insects with smooth adhesive pads [tested in cockroaches and stick insects, 57, 58, 115], but in some cases, directionality is retained, likely due to anisotropic surface sculptures or the complex fibrous ultrastructure characteristic of smooth pads [64, 81, 116, and see Fig. 5]. In hairy pads, in contrast, the reduction is much weaker because of the direction-dependence at the level of individual setae, which is based on their angled orientation and non-parallel tips [12, 57].

Conclusions

The ability of many animals to climb on vertical and even inverted surfaces has struck scientists with awe for centuries, and is a hallmark of dynamic biological adhesive systems. Strong adhesion is achieved by maximising the amount of energy needed for the creation of new surfaces; rapid detachment, in turn, requires the exact opposite. Controlling adhesion on short timescales hence requires combining two opposing demands. The shear-sensitivity of dynamic biological adhesive systems is an ingenious strategy to solve this conundrum, as it effectivly uses the same mechanism to achieve both: during attachment, elastic energy is stored in the attachment systems, but cannot drive detachment, as the active application of a stabilising force renders continued pad attachment energetically favourable. During voluntary detachment, climbing animals can actively use the stored strain energy to trigger pad detachment, and thus effortlessly detach their feet. Further research will uncover more of the fundamental physical principles underlying this core property, which will enable the rationale design of strong yet highly dynamic bio-inspired adhesives.

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